

**Autumn water sources for understory
vegetation and fungi in a boreal forest:**

- An evaluation using stable isotopes

*Höstens markvattenkällor för svamp – och undervegetationen i
boreala skogar: - En utvärdering med stabila isotoper*



Foto. Javier Segura

Javier Segura



Examensarbeten

2013:5

Institutionen för skogens ekologi och skötsel

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ISSN 1654-1898

Umeå 2013

Sveriges Lantbruksuniversitet / *Swedish University of Agricultural Sciences*

Fakulteten för skogsvetenskap / *Faculty of Forest Sciences*

Jägmästarprogrammet / *Master of Science in Forestry*

Examensarbete i markvetenskap / *Master degree thesis in Soil Science*

EX0711, 30 hp, avancerad nivå/ *advanced level A2E*

Handledare / *Supervisor*: Ulrik Ilstedt

SLU, Inst för skogens ekologi och skötsel / *SLU, Dept of Forest Ecology and Management*

Bitr handledare / *Assistant supervisor*: Niles Hasselquist

SLU, Inst för skogens ekologi och skötsel / *SLU, Dept of Forest Ecology and Management*

Examinator / *Examiner*: Anders Malmer

SLU, Inst för skogens ekologi och skötsel / *SLU, Dept of Forest Ecology and Management*

I denna rapport redovisas ett examensarbete utfört vid Institutionen för skogens ekologi och skötsel, Skogsvetenskapliga fakulteten, SLU. Arbetet har handledts och granskats av handledaren, och godkänts av examinator. För rapportens slutliga innehåll är dock författaren ensam ansvarig.

This report presents an MSc/BSc thesis at the Department of Forest Ecology and Management, Faculty of Forest Sciences, SLU. The work has been supervised and reviewed by the supervisor, and been approved by the examiner. However, the author is the sole responsible for the content.

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Abstract

Understory vegetation and fungi are regarded as important ecological drivers of processes like productivity and nutrient cycling in boreal forests. Whilst those processes are linked to soil water content, relatively little is known about the sources of soil water for these forest components. During early autumn in boreal forests, temperature falls and large events of rain are frequent which may influence soil water availability. To better understand the autumn plant-soil-fungi water relationships in this ecosystem, I used stable isotopes techniques in this study to examine the water sources for ericaceous shrubs and fungi in a Scots pine forest following a large, early autumn rain event. I hypothesize that ericaceous shrubs of two functional groups (evergreen vs. deciduous) utilize different soil water sources as a result of differences in their morphology. I also hypothesize sporocarps of saprotrophic and ectomycorrhizal fungi utilize different water sources based on previous studies that have shown a vertical separation of these fungi within the soil profile. My isotopic results showed xylem water $\delta^{18}\text{O}$ values did not differ between evergreen and deciduous shrubs (means ranged between -9.25 and -9.98 ‰). Using a two source mixing model, it appeared that saprotrophic fungi drew 20-100 % of its water from shallow sources (organic matter -1 cm deep), whereas in general, ectomycorrhizal fungi used deeper water sources (4-75 cm deep). Moreover, rather than using water at different depths, uptake patterns and sources of water for understory vegetation and fungi appeared to be greatly influenced by a large rain event that occurred two weeks prior to sampling. This study clearly shows the importance of autumn large rain events for understory vegetation and highlights the need for further examining if the mechanisms observed are the same year to year. Therefore, more comprehensive studies integrating seasonality, soil water availability and the phenological characteristics of the plants and fungi would provide a more integrated picture of the soil water-plant-fungi continuum in the boreal forests.

Keywords: *Ericaceous shrubs, fungi, Pinus sylvestris, rain event, soil profile, water stable isotopes.*

Sammanfattning

Undervegetation och svampar betraktas som viktiga, drivande ekologiska komponenter för processer som produktivitet och näringsomsättning i boreala skogar. Medan dessa processer är kopplade till markens vattenhalt, relativt lite är känt om källorna till markvatten för dessa skogskomponenter. Under början av hösten är fallande temperaturer och stora regnmängder vanliga, vilket kan påverka markvattnets tillgänglighet. För att bättre förstå höstens vattenrelationer mellan växt -jord-svamp i detta ekosystem, använde jag stabila isotops tekniker i denna studie, för att undersöka erikaceer och svampars vattenkällor i en tall skog, efter att ett stort regn inträffat under tidig höst. . En hypotes var att de två funktionella grupperna av ljungväxter (vintergröna vs lövfällande) använder olika markvattenkällor på grund av skillnader i deras morfologi. En annan hypotes var att fruktkroppar av saprotrofiska och ectomykorrhiza svampar använder olika vattenkällor, baserat på tidigare studier som har visat en vertikal separation av dessa svampar i markprofilen. Mina isotopiska resultat visade att xylem-vatten $\delta^{18}\text{O}$ -värden inte skiljer sig mellan vintergröna och lövfällande erikaceer och varierade mellan -9,25 och -9,98 ‰. En två-käll-blandning modell visade att saprotrofiska svampar utvann 20-100% av sitt vatten från ytliga källor (organiskt material -1 cm djup), medan ectomykorrhiza svampar generellt använde djupare vattenkällor (4-75 cm djup). Istället för att använda vatten på olika djup, påverkades upptagningsmönstret och typen av vattenkällor för undervegetationen och svampar i hög grad av ett stort regnfall som inträffade två veckor före provtagningen. Denna studie visar tydligt betydelsen av stora regnfall för undervegetationens vattenupptag och understryker behovet av att ytterligare undersöka om de observerade mekanismerna är desamma år efter år. Fortsatta studier bör integrera säsongsvariationer, markvattnets tillgänglighet samt växters och svampars fenologiska egenskaper, vilket kan ge en mer samlad bild av markvatten-växt-svampar kontinuum i boreala skogar.

Nyckelord: *Ericaceous shrubs, fungi, Pinus sylvestris, rain event, soil profile, water stable isotopes.*

Introduction

The source of available water for vegetation is of ecological importance because it may regulate plant productivity and survival (Plamboeck et al. 1999; Allen 2011; Moyano et al. 2012). The water used by forest understory and canopy trees may be taken up from different depths in the soil profile following patterns that are largely regulated by inherent physical characteristics of the soil as well as morphological traits of the plants (Gat 1998). Vegetation research in boreal forests has identified the understory as an important driver of above and belowground processes ultimately affecting plant communities and ecosystem properties (Nilsson and Wardle 2005). Wardle et al. (2003) had shown that the understory of a boreal forest could have a net primary production similar to that of the overstory. Further, understory vegetation has been reported to account for a significant proportion (15-50 %) of total forest evapotranspiration, which is an important component in the land-atmosphere interface of the hydrological cycle (Black and Kelliher 1989; Grelle et al. 1997; Gat 1998 in Griffiths 1998; Iida et al. 2009). Whereas most nutrients used by plants are found in the soil solution, which in turn is linked to the water content of the soil (Fisher and Binkley 2000), relatively little is known about the distribution of water sources used by understory vegetation in boreal forests.

Boreal forests are often present on Podzol soils characterized by slow rates of organic matter decomposition and scarcity of accessible nutrients, mainly nitrogen (N), for plant growth (Makkonen and Helmisaari 1998; Rosling et al. 2003). The main vascular plants growing upon these soils, the ericaceous dwarf shrubs, is the dominant component of the understory in boreal forests of northern Sweden. Among them, lingonberry (*Vaccinium vitis idaea* L.) and bilberry (*Vaccinium myrtillus* L.) are the most common species. The proportion at which these species occur is suggested to be constrained by abiotic and biotic factors regulated by the forests successional stage (Nilsson and Wardle 2005). Other studies have highlighted the importance of light conditions and/or moisture availability (Mäkipää 1999); anthropogenic activities or windthrows (Kuuluvainen 1994; Engelmark et al. 2000) and the time elapsed since last fire disturbance (Niklasson and Granström 2000) to explain the relative abundance and distribution of understory species. According to Read et al. (2004), the traits displayed by the shrubs and their corresponding mycorrhizal symbionts have coevolved to the point of being a major feature of boreal forest ecosystems.

The main mechanisms by which water is accessible to plants are the growth of roots into moist soil areas creating water potential gradients and the capillary movement of the soil water towards the root surfaces (Brady and Weil 2008). Studies have shown that in boreal forests, a significant proportion of the fine roots of ericaceous shrubs, such as *Calluna vulgaris*, are confined to the humus layer and the uppermost mineral soil (Kalela 1949; Persson 1978 and 1983). Further, as shown by Valenzuela-Estrada et al. (2008), root systems of the genus *Vaccinium* are highly branched and constituted particularly by fine roots. Differences between aboveground traits exhibit by some ericaceous dwarf shrubs (i.e. *Empetrum hermaphroditum* and *Vaccinium myrtillus*) can be posed as extreme ends of a gradient. Whereas *E. hermaphroditum* develops small, slow growing evergreen leaves, loaded with defensive substances, *V. myrtillus* develops relatively fast growing deciduous leaves, which contain low levels of defensive substances. The traits of *Vaccinium vitis idaea* can then be situated at the middle of this gradient (Nilsson and Wardle, 2005). Based on the differences between shrubs morphology, it is interesting to evaluate if they also use different water sources within the soil profile.

A large number of studies have shown that in the interface between plants dominating this biome and these recalcitrant and poorly decomposed soils, ectomycorrhizal (EM) and saprotrophic fungi play key roles in the cycling of carbon and nitrogen (Högberg et al. 2003, Rosling et al. 2003; Read et al. 2004; Lindahl et al. 2007). However, much less is known about the patterns of uptake and sources of water for both functional groups. There is evidence that EM fungi can transport water over significant distances (Duddridge et al. 1980; Brownlee et al. 1983) and mobilize readily usable nitrogen, providing their hosts with an otherwise limiting nutrient (Read 1991; Read et al. 2004) in exchange for carbon from their hosts (Högberg et al. 2001). Saprotrophic fungi are described as main degraders of forest litter and wood obtaining their energy by decomposing dead organic matter (Rayner and Boddy 1988). Further, Lindahl et al. (2007) have shown that saprotrophic and EM fungal communities display a spatial separation within the soil profile (i.e. the EM normally located in the older, more decomposed litter and humus layer, whereas saprotrophic fungi are found near the soil surface). Moreover, in podzols of the boreal forest, there is a significant variation in the composition of EM species between horizons (Rosling et al. 2003). One way to examine if the water relations of both saprotrophic and EM fungi differ is studying their epigeous sporocarps, which in northern Sweden mainly emerge during autumn.

Plant and fungi water sources partitioning has been the subject of previous studies (Dawson and Ehleringer 1991, 1996; Dawson 1996, Dawson et al. 2002; Thorburn and Ehleringer 1995; Brunel et al. 1997; Plamboeck et al. 1999; Lilleskov et al. 2009). In the northern Swedish boreal context, these studies have mainly focused on trees during the peak of the growing season (Bishop and Dambrine 1995; Plamboeck et al. 1999). Conversely, little attention has been given to the patterns of water uptake by understory vegetation and fungi in general and moreover few studies have examined water sources during the fall months. In the early autumn, falling temperatures and large rain events are frequent (SMHI 2012) which may influence soil water availability and uptake patterns of the forest understory vegetation. Within the frame of a projected changing climatic scenario for Northern Sweden fewer but more extreme events of rain can occur at the end of the growing season (SMHI 2012). A better understanding of the soil water sources for this relevant forest component in the autumn can expand our insight into the plant-soil-fungi water relationships in the boreal forest.

A constrain in assessing the order of magnitude of the uptake and exchange of water between soil, fungi and plants has been finding adequate methods to investigate the sources of water in first the place (Plamboeck et al. 2007). However, recent advances using stable isotopes technique has proven useful in determining sources of water used by individual plants and fungi in diverse natural environments (Dawson and Ehleringer 1991; Dawson and Ehleringer 1993; Dawson 1996, Dawson et al. 2002; Thorburn and Ehleringer 1995; Brunel et al. 1997; Plamboeck et al. 1999; Lilleskov et al. 2009; Plamboeck et al. 2007; Hasselquist et al. 2010). The central idea behind this technique is that the oxygen isotopic signature (^{18}O) of plant xylem water reflects the ^{18}O signature of soil water sources utilized by plants (Brunel et al. 1997). The ^{18}O signature of soil water near the surface is largely influenced by precipitation events that in turn are affected by evaporative enrichment, thereby leading to high ^{18}O values. In contrast, the ^{18}O signature of soil water found at deeper depths typically consists of deep water inputs and/or storage (in boreal forests mainly constituted by snowmelt) and is characterized by low ^{18}O values. Using these differences in the ^{18}O signature found throughout the soil profile, it is possible to determine whether or not plants are using shallow or deep water sources (Gat 1996; Dawson and Ehleringer 1998).

The plant-soil isotope technique relies upon two pivotal assumptions: 1) there is no fractionation of water during water uptake by roots and 2) there is no change in the isotopic signature of xylem water within the woody plant tissue. This implies that the isotopic signature of xylem water within woody plant tissue reflects the isotopic signature of areas in the soil from where plants extracted water (Brunel et al 1997; Dawson and Ehleringer 1991). Moreover, fungal sporocarps can be used to assess sources of water exploited by fungi as demonstrated by Lilleskov et al. (2009).

Aim and hypotheses

The aim of this study was to determine the water sources for ericaceous shrubs and fungi in a *Pinus sylvestris* forest following large, early autumn rain events in northern Sweden. I will therefore use stable isotope techniques to obtain and evaluate the isotopic signature of soil, plant and fungal material relevant for this study. I hypothesize that:

1) Ericaceous shrubs utilize different soil water sources

as a result of differences in their morphology. More specifically, because *Calluna vulgaris* (L) Hull, *Vaccinium vitis idaea* (L) and *Empetrum hermaphroditum* (Hagerup) are evergreen shrubs with small, waxy leaves adapted to prevent water loss, whereas *Vaccinium myrtillus* (L) is a deciduous shrub with larger leaves, I hypothesize that *V. myrtillus* utilizes deeper, more reliable water sources, compared to *C. vulgaris*, *V. vitis idaea*, and *E. hermaphroditum*.

2) Sporocarps of saprotrophic and EM fungi utilize different soil water sources within the soil profile. More specifically, because of the vertical separation of saprotrophic and EM fungi within the soil profile, I hypothesize that saprotrophic fungi utilize water in the upper layers of the soil profile, whereas EM fungi use deeper water sources (Fig. 1).

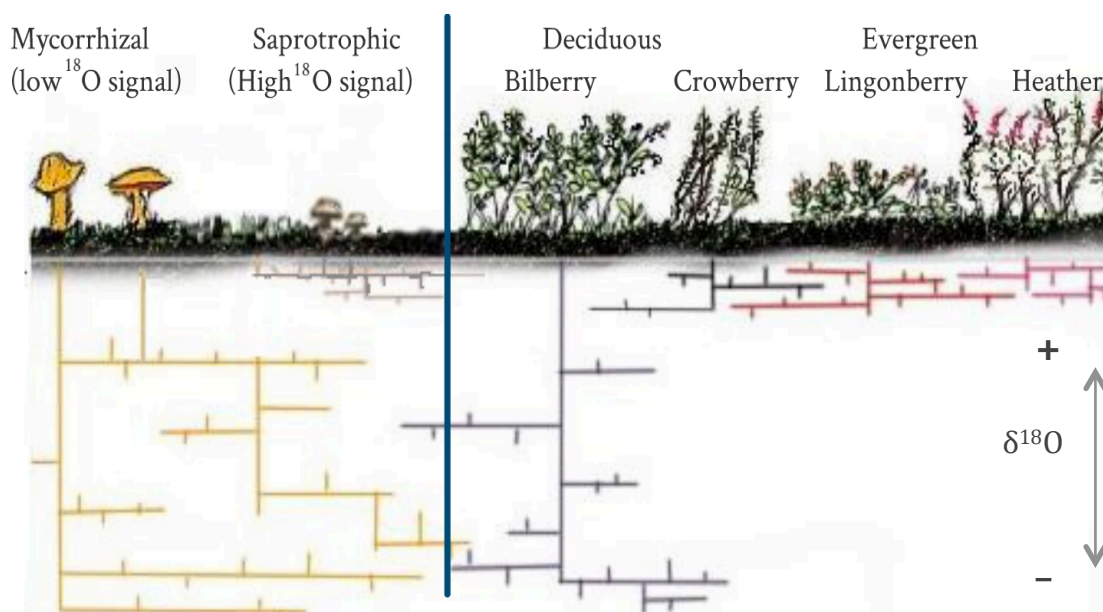


Figure 1. Graphic representation of the hypotheses examined in this study.

Materials and Methods

Study site

The study was conducted at the Rosinedalsheden experimental forest, 3 km southeast of Vindeln, Northern Sweden (64°2' N, 19°7' E; Fig. 2). The study site is characterized by a 70 year old, even-aged stand of Scots pine (*Pinus sylvestris* L.). The understory vegetation is dominated by ericaceous dwarf shrubs including lingonberry (*Vaccinium vitis idaea* L.) and bilberry (*Vaccinium myrtillus* L.), heather (*Calluna vulgaris* L. Hull) and to a lesser extent crowberry (*Empetrum hermaphroditum* Hagerup.). The bottom layer is dominated by stair-step mosses (*Hylocomium splendens*); feather mosses (*Pleurozium schreberi*) and reindeer lichens (*Cladonia* sp.) with the last ones less regularly distributed. Saprotrophic and ectomycorrhizal sporocarps were distributed sporadically across the site.



Figure 2. Location of Rosinedalsheden experimental forest, Vindeln, Northern Sweden.
Photo: N. Hasselquist.

Mean annual temperature at the site is 1.5°C and precipitation averages 591.3 mm according to the long-term temperature and precipitation series (SMHI normal period (1961-1990) series). Approximately 35% of the precipitation falls as snow during October to May. The mean monthly temperatures for the four months previous to sampling (June-September 2012) at Rosinedalsheden were 11, 14.9, 12.8, and 7.7 °C respectively. Cumulative monthly precipitation averaged 134.3, 83.7, 101.1 and 66.8 mm respectively.

The temperatures for the growing period were close to the monthly long-term mean but precipitation means for the whole period were wetter than normal (SMHI normal period (1961-1990) series). The mean daily temperature during late August and early September where was close to 10 °C. However, both the previous and the actual day of collection, temperatures rose to 13.2 and 11.9 °C respectively. Two weeks prior to the sampling, a single rain event of 46.7 mm occurred, which represented 8% of the total precipitation recorded from June to October. The soil type is classified as a ferric podzol which is relatively poor in nutrient available for plants and contains glaciofluvial soil > 50% sand (FAO-UNESCO 1988).

Experimental design and sampling

On September 12, 2012, two weeks after a large rain event, I randomly established 4 blocks (5 x 5 m) at the site, wherein I collected replicates of plant, berries, fungi and soil samples for isotopic analyses. Within each block, I collected woody tissue from four ericaceous species: *Calluna vulgaris* (L) Hull, *Vaccinium vitis idaea* (L), *Vaccinium myrtillus* (L) and *Empetrum hermaphroditum* (Hagerup). I also collected fruits from *V. vitis idaea*, *V. myrtillus* and *E. hermaphroditum* in order to examine if ¹⁸O signature in berries matched the ¹⁸O signature of xylem water. Soil samples for water content and isotopic analyses were also taken at two points within each block and at different depths (organic matter, 1 cm, 4 cm, 10 cm and 30 cm into the mineral soil). Nearby two of the blocks, deeper pits were dug to collect soil samples at 75 cm depth.

Moreover, I identified and collected cap tissue of saprotrophic and ectomycorrhizal sporocarps in and nearby the blocks. Genera of saprotrophic fungi included *Cystodérma* sp. and *Paxillus atrotomentosa* (Batsch) Fr., whereas EM species included *Cortinarius traganus* (Fr.), *Cortinarius brunneus* (Pers.) Fr., *Cortinarius semisanguineus* (Fr.) Gillet and *Lactarius rufus* (Scop.) Fr. At the time of the collection, every individual sample was inserted into 8 x 70 mm test tubes with straight rim, sealed with Parafilm® and preserved in a cool bag for transport to the university (located approx. 55 km away from the study site). Once there, the samples were kept frozen (-14°C) until further treatment. Precipitation samples for isotopic analysis were obtained from the Svartberget research station located approx. 10 km away from Rosinedalsheden experimental forest.

Extraction line and isotopic analysis

Extraction of water from soil, stem, berry and fungal tissue was performed using a cryogenic vacuum distillation line (Ehleringer et al. 2000; West et al. 2006) at the soil physics laboratory, Department of Forest Ecology and Management (Swedish University of Agricultural Sciences, Umeå). Extraction times ranged between 40 min for stems to 30 min for soils, fruits and fungi. Thereafter, the water extracted from the samples was pipetted from the extraction line's collection tubes into 32 x 11.6 mm vials and kept frozen (-14 °C) until further isotopic analyses. For precipitation samples, water was pipetted from collection containers into vials, and kept refrigerated until isotopic analyses. Since all water samples in my study are within the range of precipitation inputs and fall on the local meteoric water line of the study area, likely no fractionations were occurring (in agreement with Brooks et al, 2010).

Isotopic analyses were made using a Picarro L1102-i Isotopic Water Liquid Analyzer at the instrument laboratory, Department of Forest Ecology and Management (Swedish University of Agricultural Sciences, Umeå). This device uses a Wavelength-Scanned Cavity Ringdown Spectroscopy (WS-CRDS) to scan the absorption lines distinctive to H_2^{16}O , H_2^{18}O , and HD^{16}O . The raw data for all samples obtained from this instrument was treated following the procedure created by Ohlsson (2011), Swedish University of Agricultural Sciences, Umeå. The procedure includes correcting data for a memory effect and averaging results from individual vials. Moreover, data was sorted and corrected for drift after being calibrated against measured values from standard samples. Data is expressed as deviations from the Vienna Standard Mean Ocean Water (VSMOW) in δ notation (‰). Precision between batches was 0.04‰ for $\delta^{18}\text{O}$ and 0.15‰ for $\delta^2\text{D}$.

Isotopic correction on water extracted from fungi

Because the ^{18}O signature of fungal sporocarps were enriched relative to soil surface water, I used the methodology described by Lilleskov et al. (2009) to determine the relative enrichment of the sporocarps against the surface soil (top 10 cm) ^{18}O signature and corrected fungal sporocarp isotopic signatures to reflect their sources.

Calculations and statistical analysis

The gravimetric water content for the mineral and organic soil samples were obtained and calculated as:

$$W_g = (W_b - W_a)/W_a \quad (1)$$

where W_b equals the mass of the wet sample and W_a is the mass of the oven-dried soil. In this study, the mass of the oven-dried soil was replaced by the mass of the sample after the extraction, making the assumption that all water has been extracted. Weighing controls performed at the start, middle and end of the extraction process confirmed this assumption. The per cent water holding capacity for the organic matter was obtained by placing the material on a plastic mesh into a plastic funnel and saturating it with water for ½ h. The organic matter was then drained for ½ h until no more water was dropping. The water holding capacity was then calculated as for gravimetric water content (eq. 1) (Ilstedt et al 2000).

Statistics were run with Minitab® 16 statistical programme (Norsys Technology AB, Sweden). Isotopic data was tested for normality using the Anderson-Darling test. Differences between functional groups (i.e. between evergreen and deciduous shrubs as well as between saprotrophic and ectomycorrhizal fungi) and between the shrubs and respective fruits were examined using one-way analyses of variance. Similarly, analyses of variance were performed in order to evaluate possible differences within the soil profile. A posterior Tukey's test was performed in order to evaluate significant ($P < 0.05$) differences among means. The main data obtained in this study included the ^{18}O signature of water from ericaceous woody stems and fruits, soils at different depths throughout the soil profile, and caps of ectomycorrhizal and saprotrophic fungi.

The corrected signatures of the sporocarps were related to possible soil water sources to assess the likelihood of different depths to contribute to the mixture of water used by the fungi. Acknowledging the differences between the ^{18}O signature of shallow layer of the soil (organic matter-1 cm into the mineral soil) and the ^{18}O signature found at deeper layers (>4 cm into mineral soil), two source pools (shallow and deep) were first created. To assess the source partitioning for the two fungal functional groups, multiple source partitioning models were used. Possible water sources for the two fungal functional groups were examined using the IsoError 1_04, Microsoft Excel 2000™ spreadsheet (Phillips and Gregg 2001), which for stable isotope analyses, enables to calculate the proportions of various sources in a mixture.

Results

Figure 3 shows the daily precipitation isotopic signature of the rain during late August and early September fluctuated between -13.1‰, corresponding to the large event of rain in late august, to -6.9‰ corresponding to the day of sampling.

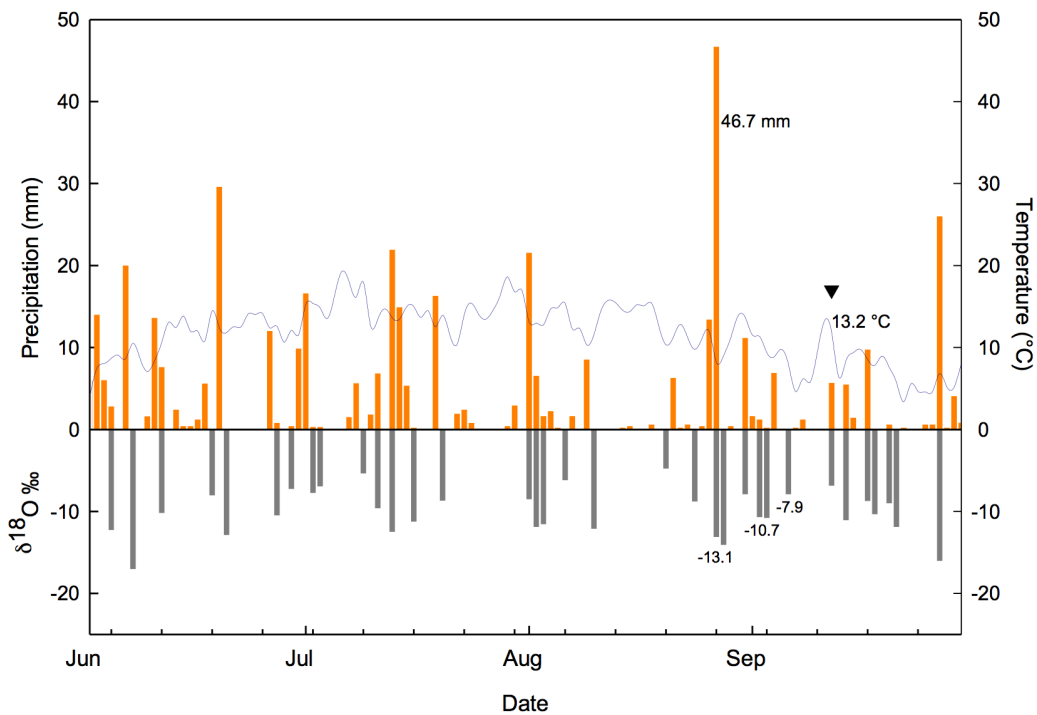


Figure 3. Daily precipitation (orange bars) and temperature (solid line) distribution during June-September 2012 at Rosinedalsheden experimental forest, Vindeln, Northern Sweden. The daily distribution of the ^{18}O isotopic composition of the precipitation during the same period was sampled at Svartberget experimental station (the inverted triangle shows the 12th of September, the day of sampling).

Soil $\delta^{18}\text{O}$ decreased gradually with depth in the profile with means ranging from -11.5 ‰ in the organic matter to -12.9 ‰ at 75 cm. At 1 cm depth (still in the organic layer), the signature peaks to -11.2 ‰, corresponding to the most enriched value in the soil profile (Fig. 4a). There were significant differences in the ^{18}O signature of soil water between 1 cm and 10 cm and between 1 cm and 75 cm depth ($P = 0.017$). There was a steep decrease in soil water content (i.e. gravimetric water content per gram dry soil) with soil depth (i.e., > 200% in the organic layer and < 20% at 4 cm into the mineral soil). At depths greater than 4 cm the decline in water content was more gradual and was only significantly different ($P < 0.0001$) between 1 cm and 75 cm depth (Fig. 4b).

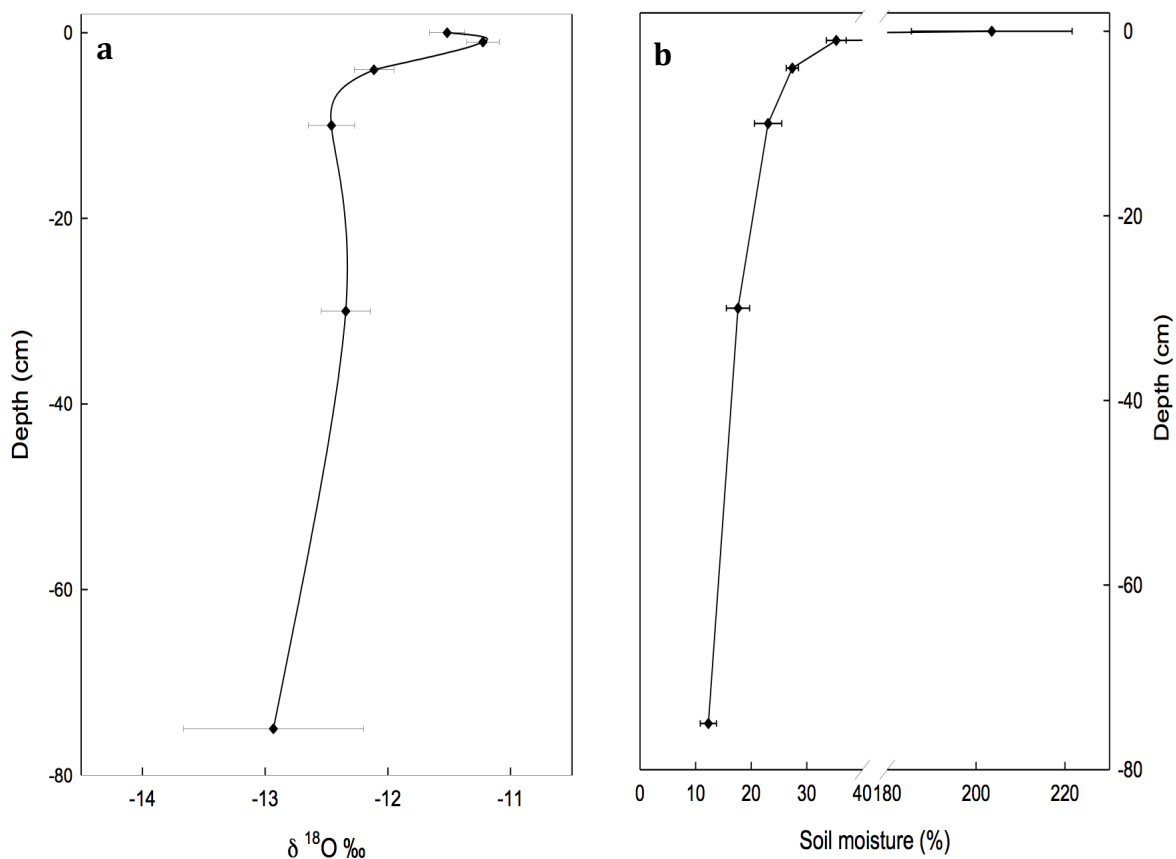


Figure 4. Mean (\pm SE) oxygen $\delta^{18}\text{O}$ isotopes signature (a) and percent soil moisture, i.e. gravimetric water content per gram dry soil (b) of the soil profile developed in a ferric Podzol at Rosinedalsheden experimental forest, northern Sweden

In general, the xylem water $\delta^{18}\text{O}$ signature did not differ between functional groups ($P = 0.607$), and their means ranged between -9.25 and -9.98 ‰. Moreover, these values were consistently enriched relative to the soil ^{18}O values, especially those found at deeper depths (Fig. 4a and Fig. 5). The mean $\delta^{18}\text{O}$ signature of water in fruits ranged between -6.67 and -7.65 ‰, and were roughly 2.5 ‰ enriched relative to xylem water found in shrubs (Fig. 5). Significant differences in $\delta^{18}\text{O}$ values were observed when comparing the signature of individual shrubs species and its corresponding fruits. For example, the signature of bilberry fruits significantly differed from that of bilberry shrubs xylem water ($P = 0.001$). Similarly, a significant difference ($P = 0.007$) was observed between the average $\delta^{18}\text{O}$ signatures of crowberry fruits and shrubs xylem water. However, no such difference was observed between lingonberry and its fruit.

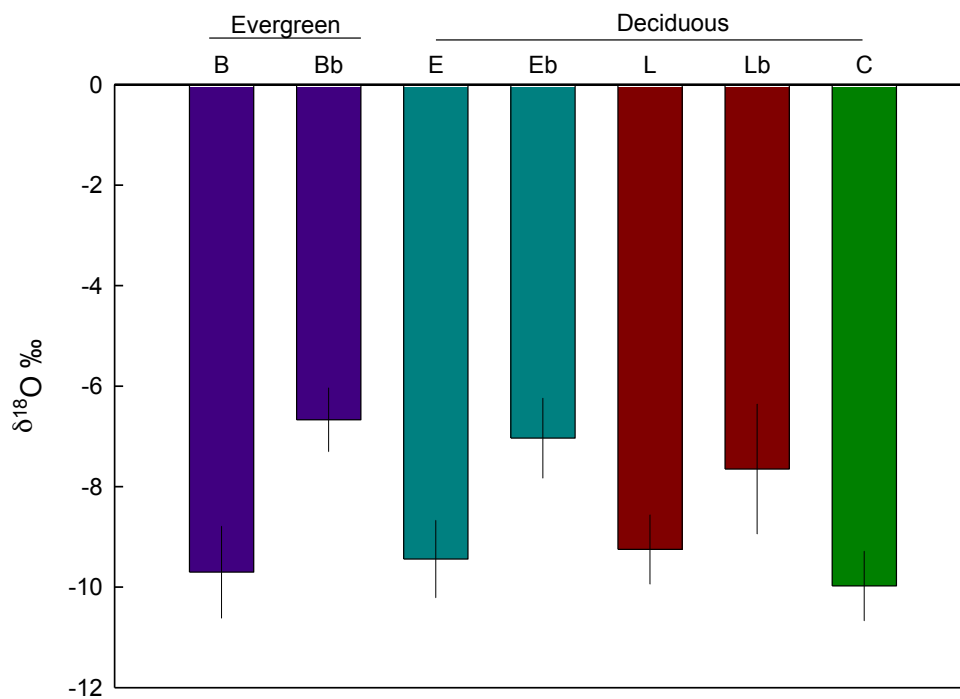


Figure 5. Mean (\pm SE) $\delta^{18}\text{O}$ isotopic signature for the two functional groups of ericaceous shrubs. B and Bb stands for bilberry xylem (*V. myrtillus*) and its fruit respectively; E and Eb for cowberry xylem (*E. hermaphroditum*) and its fruit; L and Lb for lingonberry xylem (*V. vitis-idaea*) and its fruit and C stand for heather (*C. vulgaris*).

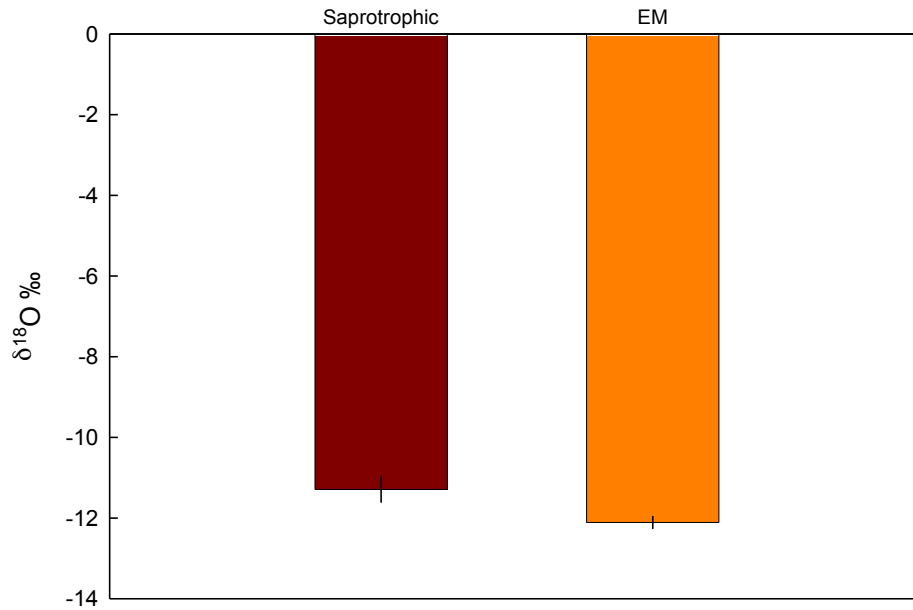


Figure 6. Mean (\pm SE) $\delta^{18}\text{O}$ isotopic signature for the two functional groups of fungi. The bar designated as Saprotrophic included only samples of *Cystodérma* sp. whereas the bar designated as EM included the species *Cortinarius traganus* (Fr.), *Cortinarius brunneus* (Pers.) Fr., *Cortinarius semisanguineus* (Fr.) Gillet and *Lactarius rufus* (Scop.) Fr.

Although not significant ($P = 0.077$) there was a general trend indicating that saprotrophic fungi caps contained relatively more enriched water (-11, 37 ‰) as compared to EM fungi caps (-12, 46 ‰) (Fig. 6). After assessing the relative enrichment of the sporocarps against the surface soil signature using the methodology proposed by Lilleskov et al. (2009), I pooled the ^{18}O signature of different depths in the soil profile. One source pool (shallow source) was formed by the signature of the organic matter layer and 1 cm into the mineral soil. The second pool (deep source) was formed by the signatures obtained from 4, 10, 30 and 75 cm into the mineral soil. According to results obtained from IsoError software it appears that 100 % of the water in the cap of saprotrophic fungi originated in the organic layer and 1 cm pool, yet this value could range between 20-100%. In contrast, it appears that sporocarps of EM fungi, in general used deeper water sources. More specifically, 65-75% of water in EM caps originated from the pool water sources > 4 cm into the mineral soil (Table 1). Moreover, the model showed that superficial sources (i.e. organic matter layer and 1 cm pool) contributed 25- 35% to the water in the caps of these fungi.

Table 1. Mean proportion (\pm SE) of shallow and deep water sources used by fungi. The lower and upper 95% confidence intervals are shown as estimated with IsoError using a single isotope, two sources approach. The pooled ^{18}O values were -11, 37 ‰ for shallow and -12, 46 ‰ for deep sources. The model calculates the proportions of various sources in a pool of isotopic signatures and takes account the variability of both pooled signatures and sources.

	Ectomycorrhizal sp			Saprotrophic sp
	<i>C. semisanguineus</i>	<i>L. rufus</i>	<i>C. brunneus</i>	<i>Cystoderma spp.</i>
Shallow source proportion [%] (SE)	0.35 (0.23)	0.25 (0.14)	0.93 (0.14)	1.07 (0.31)
95 % Confidence limits(%)	0-100	0-100	60-100	20-100
Deep source proportion [%] (SE)	0.65 (0.23)	0.75 (0.14)	0.07 (0.14)	– 0.07 (0.31)
95 % Confidence limits (%)	0-100	0-100	0-40	0-80
Sample size	5	2	5	5

Discussion

Sources of water for ericaceous shrubs

Based on differences in morphological traits between deciduous and evergreen ericaceous shrubs, I hypothesized that *V. myrtillus* (deciduous) utilizes deeper, more reliable, water sources compared to *C. vulgaris*, *V. vitis idaea*, and *E. hermaphroditum* (evergreen). My results however, show no support for such a distinction in access to different water sources. Plant roots normally access water from areas in the soil where water potentials are highest (Adar et al 1995), which in my case corresponds to the upper organic soil layer. Valenzuela-Estrada et al. (2008), suggested root systems of the genus *Vaccinium* are constituted by fine roots and are particularly highly branched. Previous studies have shown that fine roots of the genera *Calluna* and *Vaccinium* are confined to the organic and upper mineral soil layers (Kalela 1949; Persson 1978 and 1983; Makkonen and Helmisaari 1998). The $\delta^{18}\text{O}$ isotopic values of xylem water were enriched relative to all $\delta^{18}\text{O}$ soil profile values, which hindered a direct determination of water sources within the soil profile (i.e. either by direct inference or using stable isotopes mixing models). As suggested by previous studies (Dawson 1996; Yakir in Griffiths, 1998; Barbour, 2007) I utilized xylem water for isotopic analyses to minimize the effects of evaporative fractionation. Thus, the enriched signature in xylem water relative to water found throughout the soil profile cannot be explained by evaporative enrichment within plant tissue. Instead there is some evidence to suggest that understory vegetation use superficially, temporally available water from recent rain events in early autumn. On the 27th of August, a single event of 46.7 mm rained upon the site of this study. This single event, the largest recorded for the whole year, represents 64 % of the amount of rain normally falling in

the month of August (SHMI normal precipitation period 1961-90). The isotopic analysis revealed the ^{18}O value of this event corresponds to -13.1 ‰ (Fig. 3). Further, my results show the ^{18}O signature of the superficial soil layers is 1.58 ‰ enriched relative to this number. The signature I recovered from deeper soil layers is -12.93 ‰, which is certainly close to the signature of this large event (Fig. 4).

In agreement with previous studies showing soil profile gradients (Barnes and Allison 1988; Dawson and Ehleringer 1991; Dawson 1996; Lilleskov et al. 2009), the values obtained in my study follow a pattern of enrichment towards the soil surface, most likely caused by the breakup of weak bonds of lighter isotopes in the liquid phase during evaporation of the soil water at the surface level. During the period between last days of August and my date of collection (12th of September) few rain events with distinctive enriched ^{18}O values have occurred of which none could account for the isotopic soil profile or xylem water signature obtained. Thus, it appears that the depleted ^{18}O signature I observe in my study is a remnant from the large late August rain event, which probably saturated the soil profile, displaced any other signature and served as the main source of water for the shrubs. Similarly, Brooks et al. (2010) suggest a large early autumn rain event falling in a small watershed at the Cascade Mountains of Oregon, USA, could explain the depleted values observed throughout the soil profiles as well as the ^{18}O signature in tree xylem water.

One additional observation relevant to point out is that temperature at the site dropped continuously from 13.8 °C the last days of August and was as low as 4.6 °C a week later. However, during the three previous days to my collection, there was no rain and temperatures rose again and peaked at 13.2 °C the day before I conducted the sampling. I make the assumption that the evaporative demand from superficial soil layers was augmented due to the absence of rain water and the rise in temperature and that this phenomenon, at least partially, drove the water uptake pattern of the shrubs during these specific days. This indicates two major points: 1) The ericaceous shrubs were extremely responsive to the rain event two weeks previous to the sampling day and 2) rather than using water from different sources vertically in the profile, both evergreen and deciduous shrubs appeared to use superficial, readily available water. This suggests both functional groups may display a temporal based water uptake pattern during the early autumn.

At a Scots pine stand comparable to that of my study, Bishop and Dambrine (1995) found the water uptake pattern of these trees to be mainly localized to 13 cm in the soil profile. Further, Plamboeck et al. (1999) studying the same forest stand showed that, under different water supply regimes, Scots pines are rather adaptable, drawing proportionally more water

from deep layers in the soil when water becomes less available at the upper layers. In this study, I show that ericaceous shrubs, rooted in the uppermost layer of the soil, appeared to be able to take advantage of large rainfalls, especially during early autumn, to acquire water *when* and not *where* it is more available. My observations further suggest that (in concordance to the conceptualization suggested by Brooks et al. (2010)) plant-readily available water from rains that occurred previous to my sampling have not completely mixed with water in the soil profile, likely because the rain water that first wetted the soil in late August is still being held into a complex of small pores in the organic layer. Soil water content (i.e. gravimetric water content per gram dry soil) of the organic matter layer was 10 times greater than that of immediate underlying layers. Since this water content is close to the optimum conditions for microbial and plant growth (Ilstedt et al. 2000) it appeared to present a reliable source of water for the shrubs irrespective of functional group

Water sources for berries

The observed enrichment of ^{18}O berry signatures relative to xylem water (Fig. 5) is likely to be related to the intrinsic cuticle composition of berries. The cuticle of plants functions as a barrier preventing water loss from tissues to the environment (Raven et al. 2005). The cuticle is mainly composed of waxy polymers of which cutin is regarded as an important structural component (Kallio et al. 2006) constituting up to 60-80% of fruit cuticle's dry weight (Heredia 2003). Blueberry for instance, is a berry characterized by a single layer of epidermis with no stomata upon which a cuticle and a waxy blossom serve as coat (Giongo et al. 2012). In a study that examined the berry cutin composition of five species of shrubs, researchers found that *V. myrtillus* berries contain 6 % raw cutin whereas *V. vitis idaea* berries contained 30% (Kallio et al. 2006). I argue that the notable difference in cutin and hence cuticle composition between these two berries lends support to my assumption given the important role of cutin in the regulation of water loss from plant tissues. Likely, this may also explain why I do not observe a significant difference between the xylem water ^{18}O isotopic values of lingonberry and its berries. Additionally, differences in the phenology of berries may further explain the enriched ^{18}O values as bilberries and crowberries were developed and ripe one and two months earlier respectively than the berries from lingonberry (Phenological observations at Svartberget's research station). That is, berries of crowberry and bilberry had been exposed a longer period of time to water loss and subsequent enrichment relative to lingonberries.

Sources of water for saprotrophic and ectomycorrhizal fungi

The second working hypothesis I examined was whether saprotrophic fungi utilize water found in the upper layers of the soil profile, whereas EM fungi use deeper water sources. My isotope results partly lend some support for this hypothesis. I observed the ^{18}O isotopic signatures of all mushroom caps were consistently enriched relative to all possible soil water sources. Thus a direct determination of the sources of water for both fungal functional groups was impossible. However, following the methodology proposed by Lilleskov et al. (2009), I used the enrichment of sporocarps relative to surface soils in my study as a mean to apply a correction factor to the isotopic signatures to test if the sporocarps could reflect their source of water.

It is important to acknowledge that the influence of the large rain event of late august is notable in the corrected signature of both EM and saprotrophic sporocarps, as rain that occurred in the days previous to the sampling cannot account for the ^{18}O signatures recovered from both fungal functional groups. This means also that both saprotrophic and EM in my study display a spatial water uptake pattern because the ^{18}O signatures in the sporocarps are a reflection of the ^{18}O soil water signatures recovered throughout the podzol profile.

One aspect arising after employing the correction method is remarkable: Despite studying two quite different environments, the enrichment factor I calculated from my data was 6.3 ‰, which is surprisingly close to the factor calculated by Lilleskov et al. (2009). The study by Lilleskov et al. (2009) was in an alpine, drought-prone forest ecosystem receiving a total of 810 mm of precipitation annually and a mean temperature of 15,5 °C during the growing season (June –September). This study examines a mesic boreal forest ecosystem at low elevation where mean annual temperature is 1.5°C and precipitation averages 590 mm. General ecological implications are difficult to draw from this, however one arguable assumption from this result is that epigeous sporocarps may exhibit similar rates of water loss irrespective of the environment they inhabit, because water loss may be one important mechanism by which, as suggested by Lilleskov et al. (2009), sporocarps create a water potential gradient that allow them to rapidly obtain carbon from their hosts.

The results of modeling with IsoError suggest that saprotrophic fungi rely more heavily on shallow water sources as compared to EM fungi. The main source of water (spanning a range from 20 to 100%) identified in the caps of saprotrophs likely originated from the organic matter layer and 1 cm into the mineral soil.

This is in agreement with previous results showing that saprotrophic fungi occupy the upper layers of the forests floor (Lindahl et al. 2007) and given the small diameter of its mycelia, have a large surface area and access to water held even in small pores of the organic matter layer (Finlay et al. 2009). Additionally, it is known from previous studies that saprotrophic fungi dominate the recent, undecomposed soil surface both colonizing and utilizing energy-rich, recently fallen litter, outcompeting EM fungi from the upper soil horizons (Colpaert and van Tichelen 1996; Lindahl et al. 2007). Although the model showed that saprotrophic fungi may also be utilizing some deeper water sources, this is probably explained by the similarity between the ^{18}O values of shallow (-11, 37 ‰) and deep (-12, 46 ‰) source pools (Table 1.) which were used to run the model. Although a two sample t-test revealed these two pooled signatures were significantly different ($P = 0.017$), it is probably a consequence of the pooling of source signatures which facilitated the use of IsoError to identify the proportion each source contribute to a specific individual fungi. Yet, based on my results, I cannot rule out that saprotrophic fungi are utilizing deeper water sources.

In contrast, my results showed EM fungi as a functional group appeared to use deeper water sources relative to saprotrophic fungi. This finding is consistent with the study by Rosling et al. (2003), who showed the root tips of EM where not only present in the organic matter layer but also two thirds of all root tips occurred and were associated with the mineral soil. However, looking at the EM fungi species level, the results are more contrasting. More specifically, 65 % ($\text{SE} \pm 0.23$) of the water in the cap of *Cortinarius semisanguineus* species and 75 % ($\text{SE} \pm 0.14$) of water in the cap of *Lactarius rufus* species originated from sources ≥ 4 cm into the mineral soil. Contrastingly, the model showed the species *Cortinarius brunneus* obtained 92% ($\text{SE} \pm 0.14$) of its water from sources at a depth between the organic matter layer and 1 cm into the mineral soil (Table 1). These results are indeed contrasting, yet in line with previous findings. In their paper, Genney et al. (2006) showed that mycelium of *Cortinarius spp.* extent often from deeper soil horizons colonizing tissues of dead mosses in shallower layers. Thus, the EM isotopic values obtained in my study are reflecting the distribution of the mycelia of EM fungi, which can extent several horizons within the soil profile. Consequently, my results showed that both EM and saprotrophic fungi tended to use more or less spatially separated sources of water resembling their dominance in different horizons of the soil profile.

Whilst the proximity of the ^{18}O signatures obtained from both functional groups reflects their close and complex interactions, Koide and Wu (2003) have suggested that some of the competitive interaction between EM and saprotrophic fungi indeed may be the result of competition for water between EM and saprotrophic mycelia.

Conclusions

My results indicate that the uptake pattern and sources of water for understory vegetation and fungi in boreal forests are greatly influenced by punctuated, large rain events falling in early autumn in northern Sweden. This is evident by the fact that the water extracted from soil profiles largely retained the ^{18}O isotopic signature characteristic of the first big autumn rainfall and none of the rains previous to my sampling had ^{18}O values that could account for the isotopic soil profile observed. Interestingly, rather than using water from different depths, both evergreen and deciduous shrubs appeared to use superficial, readily available water from the first autumn rainfalls, suggesting both functional groups display a temporal based water uptake pattern during the early autumn. Further, this study shows a general trend in the water sources used by saprotrophic and EM fungi, which reflects their dominance in different horizons of the soil profile. It is important to point out that this study is framed within a restricted time window which allowed for a single occasion sampling during autumn. Thus, there is the need for further evaluation to see if the mechanisms observed are the same year to year and to examine if the large rain events have effects extending from one year to the next. Moreover, the strength of the result can be improved by examining the patterns of uptake and sources of water in spring and summer. Given that temperature and precipitation in those seasons are different, plant and fungi phenological characteristics, soil water availability and the mixing of water in the layers of the soil would provide an integrated picture of the plant-soil-fungi water dynamics in the boreal forests.

Acknowledgments

I would like to extend my gratitude to Ulrik Ilstedt, Niles Hasselquist, Natxo Garcia, Andres Peralta Tapia and Aida Bargaúes for assistance and guidance during the process of writing this thesis. Thanks to my little big family and friends who have been there to support me.

Para A&A.

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